SPECIES RICHNESS OF RECENT SCLERACTINIA

BY

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ABSTRACT

Most previous estimates of the number of valid, described Recent species (known species richness) of Scleractinia have been unsupported guesses ranging from 1000-2500 species. The actual number, based on a list of all senior synonyms, is approximately 1314, classified in 24 families and 220 genera (average number of species per genus = 5.97), 79 of the genera being monotypic. The numbers of zooxanthellate and azooxanthellate species and genera are about the same: e.g., zooxanthellates contributing to 48.2% of the genera and 49.5% of the species. Over the last three decades an average of 16.1 new species of Scleractinia have been described each year. Although the yearly rate of new descriptions is very uneven, the decadal trend appears to indicate a gradual decrease in the number of newly described zooxanthellate species and genera, balanced by an increase in the number of newly described azooxanthellate species and genera. An estimate of total species richness was made based on the perceived ratio of described to undescribed species of Scleractinia ascertained from the analysis of comprehensive faunistic analyses and taxonomic revisions. This method estimates a minimum of 1479 species. A second, less reliable method, which is based on the rates of species descriptions over time, suggests a range of 1460-2628 species.

EPIGRAPH

"There are about 2500 living species of corals and over 5000 extinct ones; hence these animals reached their height in past ages and are now on the decline." (Hyman, 1940: 620)

KNOWN SPECIES RICHNESS

Historical Estimates

Estimates of the number of valid, described, living (modern) species of Scleractinia range from a low of 1000 (Kaestner, 1964) to a high of 2500 species (Hyman, 1940)(see Table 1). Most of these estimates are educated guesses, not accompanied or based on a listing of actual species names that would allow for hypothesis testing and constructive criticism. The first publication purporting to list all scleractinian species was that of the World Conservation

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Table 1.–Estimates of Known and Total Species Richness of Scleractinia

Year	Author	Zooxanthellate I-Pac	Zooxanthellate Atl.	Zooxanthellate Total	Azooxanthellate	Total
Estimates of Known Species Richness:						
1925: 825	Kükenthal	-	-	-	-	2500
1940:620	Hyman	-	-	-	-	2500
1943: 77-90	Vaughan & Wells	>500	48	548	~453	>1001
1956: 360	Wells	>500	-	-	-	-
1967:115	Kaestner	-	-	-	-	1000
1967:79	Wilmoth	-	-	-	-	2500
1981:120	Rosen	500	68	568	-	-
1982:611	Cairns & Stanley	-	-	940	560	1500
1982:701	Dunn	-	-	-	-	2500
1985:37	Naumov, et al.	-	-	550	-	2500
1985: 18	Kühlmann	-	-	-	-	2500
1986: 179	Cairns, et al.	-	-	-	-	2500
1986:1	Veron	~500	-	-	-	-
1987:642,668	Chevalier	700	70	770	<850	<1620
1988: 67	Schuhmacher	500	84	584	-	-
1989: 35	Zibrowius	500	60	560	~560	~1120
1990: 206	Brusca & Brusca	-	-	-	-	2500
1991: 476	Jackson	-	-	750	-	-
1993: 60-136	WCMC	547	68	615	425	1040
1995: 160	Veron	-	-	833	-	-
1997: 2	Cairns	-	-	-	617	-
1999 (herein)	**Cairns, Hoeksema & van der Land**	**585**	**70**	**656**	**669**	***1314**

*allows for 11 facultative species

Estimates of Total Species Richness:					
Based on partial inventory (see text)	-	-	>696	>781	>1479
Based on rate of description (see text)	-	-	-	-	1460-2628

Table 2.–Numbers of valid species (and genera), monotypic genera, and average number of species per genus of the Recent Scleractinia, arranged by family from highest number of species to lowest.

Family	Zooxan-thellate	Azooxan-thellate	*Facul-tative	Total	Mono-typic Genera	Ave. Species Per Genus
Caryophylliidae	25(10)	274(43)	3(2)	296(51)	17	5.8
Acroporidae	199(4)	0	0	199(4)	0	49.8
Dendrophylliidae	15(3)	135(17)	2(1)	148(19)	4	7.8
Faviidae	103(24)	0	0	103(24)	9	4.3
Flabellidae	0	98(10)	0	98(10)	2	9.8
Poritidae	74(4)	0	0	74(4)	1	18.5
Turbinoliidae	0	51(22)	0	51(22)	7	2.3
Mussidae	46(13)	0	0	46(13)	6	3.5
Agariciidae	45(7)	0	0	45(7)	3	6.4
Fungiidae	44(11)	0	0	44(11)	3	4.0
Rhizangiidae	1(1)	33(4)	1(1)	33(4)	0	8.3
Pocilloporidae	22(4)	10(1)	2(1)	30(4)	1	7.5
Siderastreidae	27(6)	0	0	27(6)	3	4.5
Oculinidae	14(5)	15(6)	3(1)	26(10)	7	2.6
Fungiacyathidae	0	20(1)	0	20(1)	0	20.0
Pectinidae	19(5)	0	0	19(5)	0	3.8
Micrabaciidae	0	13(4)	0	13(4)	0	3.3
Merulinidae	12(5)	0	0	12(5)	3	2.4
Anthemiphylliidae	0	7(1)	0	7(1)	0	7.0
Guyniidae	0	7(7)	0	7(7)	7	1.0
Gardineriidae	0	5(1)	0	5(1)	0	5.0
Meandrinidae	5(4)	0	0	5(4)	3	1.3
Astrocoeniidae	4(2)	0	0	4(2)	1	2.0
Trachyphylliidae	1(1)	0	0	1(1)	1	1.0
Incertae Sedis	0	1(-)	0	1(-)	-	-
TOTALS:	656(109)	669(117)	11(6)	1314(220)	79	5.97

*Facultative: Eleven species may occur in the zooxanthellate and azooxanthellate forms: three species of *Heterocyathus*, two species of *Heteropsammia*, two species of *Madracis, Astrangia poculata*, and three species of *Oculina*. These species are counted as both zooxanthellates and azooxanthellates, but only once in the total column. *Cladocora* also contains species, some of which are exclusively zooxanthellate, others exclusively azooxanthellate.

Monitoring Centre (WCMC, 1993), compiled by E. Wood for the purpose of listing all scleractinian species regulated by CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora). Although a worthy first attempt, this listing of 1040 species is considered to be flawed (uncritical) in that it used outdated taxonomy, occasionally included fossil species and genera, included some junior synonyms, and included some duplication of names. It also employed a confusing, three-tiered system of categorizing species, i.e., nominal, valid, and "well-established", and was far from complete regarding the azooxanthellate species.

The only other listing known to include all Recent scleractinian species was an unpublished draft (1995) of 1259 species submitted at the Sixth International Conference on Coelenterate Biology (ICCB VI) as part of a larger series included in the Unesco-IOC Register of Marine Organisms (ed. J. van der Land, 1995). It is that list, which is herein corrected and updated, that forms the basis for the 1314 species listed in the Appendix.

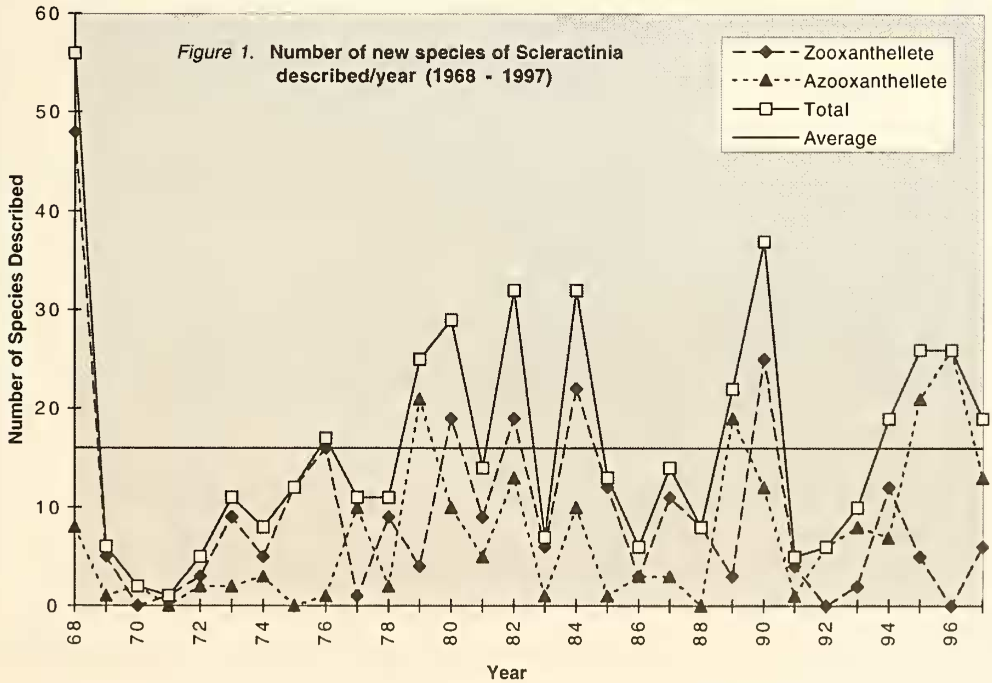
The Current Number

The current (end of 1998) number of 1314 valid, Recent scleractinian species (see Appendix), is summarized by family in Table 2. From this compilation one can see that there are 24 families of Recent Scleractinia, containing 220 genera, 79 (36%) of which are monotypic. Twelve families are exclusively zooxanthellate, 7 families are exclusively azooxanthellate, and 5 families contain genera having both ecological classes. In fact, eleven species and six genera are facultative, existing in both the zooxanthellate or azooxanthellate forms, depending on the environment (listed as a footnote to Table 2). The numbers of zooxanthellate and azooxanthellate species is virtually the same, 656 (49.5%) vs 669 (50.5%), respectively. Likewise, the number of genera is almost the same, with only a slight majority favoring the azooxanthellates at both taxonomic levels. There is an average of 5.97 and a range of 1-49.8 species per genus. Since Cairns (1997) calculated a similar species average of 5.37 for the exclusively azooxanthellate species, this ratio is approximately the same for both zooxanthellates and azooxanthellates.

It should be stated at this point that the species concept used in this paper is the morphospecies, or operational morphotaxonomic unit (sensu Veron, 1995), first formalized for scleractinian corals by Vaughan (1907: 4) as: "...a group of individuals connected among themselves by intergrading characters and separated by distinct lacunae from all other individuals or groups of individuals." Molecular, physiological, behavioral, and ecological evidence of species distinction (see Lang, 1984) were undoubtedly used to help construct the list of coral species, but these kind of data are not currently available for many species and not at all for fossil species, which makes the morphospecies most appropriate when comparing faunas within the fossil record. The "species problem" in corals is amply discussed by Veron (1995), including ramifications of reticulate evolution and the philosophy of conceptual vs operational species definitions. But, for the purposes of this paper, the traditional morphospecies is employed.

RATES OF NEW SPECIES DESCRIPTIONS

Over the last 30.5 years (1968 to mid-1998) the rate of description of new species of Scleractinia has been very uneven (Figure 1), reflecting the aperiodic publication of major faunistic revisions. (No judgment of the validity of these newly described species is made herein.) In this time interval, 490 species were described, or an average of 16.1 species per year. The uneveness of the yearly description totals is reflected in a range of 1-56 and a rather high standard deviation of 12.3. However, when viewed on a decadal scale (Table 3), some trends are apparent. Whereas the number of new species descriptions has seemed to reach a plateau over the last 20 years, the zooxanthellate:azooxanthellate components have altered dramatically. There appears to be a decline in both the number of newly described species and genera of zooxanthellate corals, which is replaced by an increase in the number of both genera and species of azooxanthellate corals. In fact, no new genera of zooxanthellate were described in the last decade, whereas 20 new azooxanthellate genera were described in the same time period. This change in rates of description might suggest that the more accessible, shallow-water zooxanthellate species are becoming fairly well known worldwide, especially at the generic level, whereas the primarily deep-water azooxanthellate fauna is less well known and thus might contribute more to the increase in described scleractinian species richness in the future.



ESTIMATES OF TOTAL SPECIES RICHNESS

Armed with these statistics on the known fauna, it is tempting to predict the total species richness of Scleractinia. One method of estimating global species richness in a taxon is the partial inventory method, which relies on the perceived ratio of described to undescribed species ascertained by a specialist in that group and/or by analysis of the literature. For instance, over the last 20 years the average percentage of previously undescribed azooxanthellate species in 14 faunistic studies from 12 regions (Cairns, 1979, 1982, 1984, 1989, 1991, 1994, 1995, 1998, 1999, in press a; Cairns & Parker, 1992; Cairns & Keller, 1993; Cairns & Zibrowius, 1997; Zibrowius, 1980) was 14.3% (range = 5.0-24.0%), or conversely 85.7% previously described. If this average described ratio is assumed to apply to the entire currently known azooxanthellate fauna (669 ÷ 0.857), one might expect there to be 781 azooxanthellate species worldwide. If similar logic is applied to zooxanthellate corals, a smaller ratio of 6.1% (range 0-18.2%) undescribed, or conversely, 93.9% previously described species results. This undescribed:described ratio is based on the following 15 publications covering six regions and two taxonomic revisions: eastern Australia (Veron et al., 1976-1984); western Australia (Veron, 1985; Veron & Marsh, 1988); Japan (Veron, 1990, 1992); Viet Nam (Latypov, 1990, 1992); Red Sea (Scheer & Pillai, 1983); Caribbean (Zlatarski, 1982); family Fungiidae (Hoeksema, 1989); and genus *Leptoseris* (Dinesen, 1980). This average described ratio applied to the known zooxanthellate fauna (656 ÷ 0.939), results in the prediction of 698 species. Together, the zooxanthellate and azooxanthellate estimates total 1479 (Table 1). To reiterate, the assumptions implicit in this estimation are: 1) 1314 currently known valid species, composed of 656 zooxanthellates and 669 azooxanthellates, and 2) a minimal undescribed component of 14.3% for azooxanthellates and 6.1% for zooxanthellates.

Table 3.–Decadal trends in rates of description of species (and genera) of Recent zooxanthellate and azooxanthellate Scleractinia. *Average for second decade corrected because Zoological Record volume 123 covered 1.5 years, making total period analyzed 30.5 years.

Zoological Record Volume	Years of Coverage	Zooxan-thellate	Azooxan-thellate	Total	Ave. Number Species/Year	Growth Rate (%)	Overall Rate
105-114	1968-77	100(6)	29(0)	129(6)	12.9	1.35	2.97
115-124	1978-87/88	114(9)	69(8)	183(17)	*17.1	1.53	3.52
125-134	1988-97/98	65(0)	113(20)	178(20)	17.8	1.35	3.25
TOTAL:	1968-97/98	279(15)	211(28)	490(43)	16.1	1.23	2.94

A second method of estimating diversity, developed by Hammond (1992), is based on an analysis of time series of species description rates. First, one calculates the current growth rate per annum of the taxon in question, i.e., the number of species described per year divided by the total number of valid species. Using the average number of scleractinian species described per year over the last 30 years (16.1) and the current total number of scleractinian species, this equation is 16.1 ÷ 1314, or 1.23%, implying that over the last 30 years the number of scleractinian species increased by about 1.23%/year, although due to synonymy this percentage is certainly lower. Decadal rates are also given in Table 3. Secondly, Hammond calculates the ratio of the current rate ÷ overall rate, the overall rate being the average yearly rate of species descriptions since 1758. Again, using the average number of scleractinian species described per year over the last 30 years (16.1) and the overall rate of 1314 species ÷ 240 years (=1998-1758), yields the equation: 16.1 ÷ (1314÷240), or 2.94, implying that over the last 30 years corals have been described at 2.94 times the post-Linnaean "average rate." Decadal rates are also listed in Table 3. Hammond then compares these two ratios (the growth rate and current rate/overall rate) with the ratios derived for other animal groups (which for scleractinian corals is coincidentally the same as that for fish), and rather subjectively designates a value for "the proportion of species described to date." According to Hammond these two ratios are consistent with taxa having a "high" proportion of previously described species, i.e., 50-90%. Applying this percentage to 1314 species results in an estimation of 1460-2628 species (see Table 2). Assumptions implicit in this estimation are: 1) 1314 currently valid species, 2) all newly described species are valid, and 3) acceptance of implications of species growth rates and overall rates as intuited by Hammond (1992).

DISCUSSION

Methods for estimating global species richness of various taxa are highly controversial, often conflicting, and usually difficult to apply. Useful reviews on this topic include: May (1990), Hammond (1992, 1994), Stork (1993, 1997), and Colwell & Coddington (1994). Some of these methods rely on the principle of taxon ratios, wherein a reference site is chosen for which one element of the fauna is thought to be fairly well known (or at least well sampled), providing an estimate of the described:undescribed species ratio for that taxon for that site. This ratio is then applied to the currently known species richness of a larger area that includes the reference site (hierarchical taxon ratio) or a separate geographic area (non-hierarchical taxon ratio) to obtain estimates of species richness. The first method used in this paper, the "partial inventory method," falls into this category and is patterned, in large part, on a study by Hodkinson & Casson (1991), who attempted to determine global insect biodiversity using a hierarchical taxon ratio. After extensive sampling of Hemiptera in northern Sulawesi, Hodkinson & Casson determined that 62.5% of the collected species were undescribed. Then, making family-by-family comparisons of Sulawesi to world species, they showed that the same proportion of new species is likely to be found worldwide. Using these ratios and the currently known species richness of Hemiptera, they were able to provide a reasonable estimate of the worldwide Hemiptera species richness. Critics of this method (Stork, 1993, 1997; Hammond, 1994) point out that it is virtually impossible to claim that all species, whether insect or corals, are known from any reference site, regardless of the intensity of collection. This is a valid criticism, and for that reason the estimates that result from such studies should be considered as minimum estimates. A second criticism of this method is the assumption that the described:undescribed ratio of one well sampled area is representative of the rest of the world. To ameliorate this criticism, I have chosen an average described:undescribed ratio from 18 regions and two taxonomic revisions, and furthermore established two different ratios, one for zooxanthellates and the other for azooxanthellates.

Hammond's method of using trends in description rate to predict global species diversity has been criticized by Erwin (1991) and Hammond (1992) himself, and is not a frequently used estimator for species richness. Rates of description depend on many factors, including one's species concept, the number of taxonomists working on a group at any period of time, and the technology used to investigate species. There also appears to be a bias to describe species of large body size and for which material is available, more commonly from temperate localities. Finally, Hammond's classification of the "proportion of species described to date" is extremely subjective (intuitive) and essentially undefined (unscientific). Also, the influence of new technology on known species richness is unpredictable. For instance, molecular analysis (allozymes) has suggested an increase in the number of *Montastraea* sibling species (Knowlton et al., 1992), whereas similar techniques have suggested a reduction in the number of recognized *Platygyra* species (Miller & Benzie, 1997); however, molecular data "have generally been found to support traditional morphological interpretations of species boundaries" (Wallace & Willis, 1994: 248; see also Willis, 1990). Synonymy of species is also a common result of more thorough morphological examination of larger suites of specimens from more diverse areas. Thus, the tendencies to increase the number of known species (e.g., discovery of sibling species) are often offset by the synonymy of species based on morphological and/or molecular methods. The overall effect is impossible to predict. Although Hammond's method is highly subjective and rarely used, it is one of the few methods available to predict total scleractinian species richness and does suggest, in my opinion, a reasonable range. On a purely intuitive basis, I would estimate the total number of scleractinian species to be about 2100, implying that we have described about 63% of the known fauna and that about 790 species remain to be described in this order.

CONCLUSIONS

What drives some people to want to know how many species exist on this planet or, more specifically, how many species occur in a particular taxon? The traditional answers are usually threefold (May, 1990; Stork, 1993). A knowledge of species richness: 1) helps establish a necessary first step to understand how biological systems work and provides a baseline that would allow for their conservation (ecology and conservation argument), 2) allows for the potential use of a greater variety of species for pharmaceutical products (utilitarian argument), and 3) satisfies the simple, unadulterated curiosity to know (quixotic argument). In addition to these traditional arguments, I would suggest that knowing the actual number of Recent scleractinian species is a valuable reference point for comparisons to late Tertiary faunas (one might call the Recent Benchmark or Paleontological Baseline argument). Hyman's (1940) conclusion that corals are "on the decline" because there are now only 2500 living species and 5000 extinct ones, is incorrect and misleading in many ways. First, there are far fewer than 2500 valid living species; it is absurd to compare taxa from the Recent to the entire Phanerozoic; comparing Mesozoic-Tertiary Scleractinia to Paleozoic Rugosa and Tabulata is illogical; and finally the total number of reef scleractinian corals appears to vacillate in time (Budd, in press) and is not a simple trend. And yet this ill-founded statement seems to have influenced two generations of textbook writers and even coral biologists (Table 1). According to Veron (1995: figs. 25, 36-38) and Scrutton (1997: fig. 2), Scleractinia stand at an all time maximum of generic diversity, but can the same be said at the species level? In very thorough studies of the Caribbean Neogene zooxanthellate Scleractinia, Budd, Stemann & Johnson (1994, Table 5) and Budd, Johnson & Stemann (1996) found 67-100% more species throughout the Late Miocene to Pliocene at 2 MY intervals than in the Recent, whereas Cairns (in press a, b) found considerably more Recent azooxanthellate species (131 species) than in the comparable Caribbean Neogene (49 species). Thus, whether the Caribbean zooxanthellates are on the decline and the azooxanthellates are on the increase, or whether the latter assumption is due to the artefact of "the pull of the Recent," it is essential to have an accurate baseline figure of Recent species richness to even begin these or similar speculations.

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